Mating Behavior of the Big-Headed Grasshopper, *Aulocara elliotti* (Orthoptera: Acrididae), Under Caged Conditions in the Greenhouse and Outdoors[1, 2]

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ABSTRACT

Daily observations of marked *Aulocara elliotti* (Thomas) at various sex ratios in cages in the greenhouse and outdoors were conducted over a 10-week period. The general mating habits of the species are described. A test for independence in mating preference in each cage revealed evidence that only 3 of the 20 cages were nonindependent at the 5% level of significance. In both study groups, the copulation frequency per male increased as the ratio of males to females decreased, possibly because of reduced competition among the males and/or to the increased availability of females which afforded greater opportunity for mating. High sexual activity by females at certain sex ratios caused reduced egg production in both groups. Males isolated from females exhibited homosexuality accompanied by occasional aggressiveness.

The big-headed grasshopper, *Aulocara elliotti* (Thomas), is one of several species of grasshoppers occurring in short-grass prairie areas west of the Mississippi (Pfadt 1949). Although it may cause widespread economic loss to rangeland, few studies concerning the biology of this species have been published. Distributon and food for it were reported by Pfadt (1949). He noted that early instars fed mainly on Sandberg bluegrass and later instars and adults on western wheat grass. Anderson and Wright (1952) and Anderson (1964) described their food habits. Anderson and Hastings (1966) discussed certain procedures involved with rearing the big-headed grasshopper in the laboratory. Roemhild (1965a, b) determined the oxygen consumption of eggs in various stages of development and the influences of cyclic temperatures on diapause termination.

The objectives of this study were to observe mating behavior and to note the influence of various sex ratios on the frequency of copulation and subsequent egg production.

MATERIALS AND METHODS

Several hundred early-instar nymphs of the big-headed grasshopper were collected from rangeland near Wheatland, Wyo., on June 6, 1964, and reared to adults in a greenhouse at Fort Collins, Colo. On the day of adult emergence they were given identifying marks on the pronotum with a nontoxic latex paint and divided into groups A and B. Grasshoppers in group A were held under artificial conditions in the greenhouse in "Montana Type" plastic circular cages with a basal area of 1 ft^2, and were fed freshly cut western wheatgrass every other day (N. L. Anderson, personal communication). Sifted soil for oviposition was provided in 9-in. paper pie plates which fitted snugly into each cage's wooden base. In group B, the grasshoppers were maintained in wire-screened cages with a basal area of 1 yd^2 under the more natural conditions outdoors and adjacent to the greenhouse and were provided with western wheatgrass grown in clay pots. Females in this group oviposited in the natural but more firmly packed clay-loam soil.

Six grasshoppers in one of the following ratios of males to females were placed in each cage: 6:0, 5:1, 4:2, 3:3, 2:4, 1:5, and 0:6. Two cages of each sex ratio were maintained within the greenhouse, while outdoors duplicates of all ratios except the 6:0 and 0:6 ratios were studied.

From 8 AM to 6 PM daily (from June 26 to September 1, 1964), observations varying from 1 to 15 min were made on the grasshoppers in each cage. The information recorded during these observations was: (1) the number of mating attempts, characterized by a male's either mounting a female but not copulating or assuming the copulatory position on another male; (2) the type of approach made by a male toward a female prior to mating; and (3) the frequency of copulation of each grasshopper. A male mounting a female and copulating for only a few seconds, then dismounting, was counted as having copulated even though it was unknown whether a spermatophore was passed.

Grasshoppers which died during the first week of the study were replaced by others isolated from the opposite sex. After the grasshoppers died, the egg pods in each cage were collected and the number of eggs within each pod counted. During the study the temperature in the greenhouse averaged 84°F, while the average relative humidity was approximately 63%. The temperature outside averaged 76°F, and the average relative humidity was 55%.

RESULTS AND DISCUSSION

General Description of Mating Behavior.—The method of copulation in the big-headed grasshopper was similar to that described by several workers for other species of grasshoppers (Federov 1927, Uvarov 1928, Husain and Mathur 1945, Srivastava 1957). In general, a male mounted a female with his forelegs

[1] Contribution from Regional Project W-37. Published with the approval of the Director of the Colorado Agricultural Experiment Station as Scientific Series Paper no. 1170. Accepted for publication December 13, 1966.

[2] From a thesis presented by the senior author in partial fulfillment of the requirements for the degree of Master of Science at Colorado State University, Fort Collins.

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clasping the lower margin of her pronotum, his middle legs attaching near the coxal area of her mesothorax, while his hind legs remained free. Once secured, the male positioned himself slightly posterior and bent the terminal portion of his abdomen downward on either side of the female, bringing his genital organs in contact with those of the female. Following coupling, the female's abdomen twisted sideways, allowing the male's abdomen to straighten somewhat, and then the male moved slightly forward.

During their random movements in the cages, males normally were attracted by the quick movements of other grasshoppers. When a male was attracted to and approached another male, both males would vibrate their hind femora for a few seconds while facing each other and then usually one moved away. At times, a male would approach a second male, brush antennae with it and depart. If a male was attracted to a female, both the male and female often would briefly flex their hind femora while at the same time the male would approach her from the side or rear and promptly mount her. Frequently, the male would briefly flex its hind femora and the female, if unreceptive, would rapidly vibrate and violently kick the male with its hind legs, then move away. The male would usually resume normal activity until attracted to another female.

According to Loher (1959), vibration of the hind femora by the desert locust, *Schistocerca gregaria* (Forskål), occurred as a visual response to movement and functioned as a warning and defensive reaction. The observations made during this study indicated that vibration of the hind femora of the big-headed grasshopper served a similar purpose.

In addition to avoiding copulation by vibrating its hind femora, a female would often elevate the terminal portion of its abdomen to prevent the male from mounting, or in many cases with the male already mounted, this elevation seemed to cause the male to become disoriented and often to reverse its position. Frequently, males were unable to mate with gravid females, since the females' abdomens were too elongated to allow the males to couple their genitalia.

Competition Among Males.—Aggressive behavior between males was observed sporadically during this study. Males were frequently noted attacking copulating males by rearing and striking them with their front pair of legs. Although Srivastava (1957) observed that male tobacco grasshoppers, *Atractomorpha crenulata* (F.), often preferred to mate with the same female and attempted to monopolize the females by frequently dislodging rival males, only a few males and females of the big-headed grasshopper exhibited a tendency to copulate several times in succession. The males never appeared to monopolize females by protecting them from mating attempts by other males.

A chi-square analysis which tested for independence in mating selectivity in each cage showed that only 1 cage at the 1:5 ratio indoors and 2 cages outdoors, 1 at the 4:2 and 1 at the 2:4 ratios, were significant at the 5% level. The analysis thus provided evidence of nonindependence in only 3 of the 20 cages, indicating that preferential mating probably is not a significant factor in the mating habits of the big-headed grasshopper.

Homosexuality.—In both groups in those cages with only male grasshoppers, homosexuality accompanied by occasional aggressive assaults were observed, although not frequently. Homosexual behavior, broadly defined in this study, occurred when a male grasshopper assumed the copulatory position over another male and probed with his genital organs along the underside of the other male's abdomen, while concurrently the lower male usually ran about trying to dislodge the aggressor.

Effect of Sex Ratio on Frequency of Copulation.—The average copulation frequencies for the various sex ratios with males and females in groups A and B during the 10-week period of study are presented in Table 1. For those grasshoppers in group A, the average copulation frequency ranged from a low of 1.3/male at the 5:1 ratio to 18.0 at the 1:5 ratio. The average number of matings per female ranged from 3.6 at the 1:5 ratio to 8.5 at the 4:2 ratio. In group B, the average number of copulations per male ranged from a low of 1.1 at the 5:1 ratio to a high of 29.0 at the 1:5 ratio. The average number of copulations per female ranged from 5.5 at the 5:1 ratio to 15.5 at the 4:2 ratio.

At all sex ratios, except the 5:1 and 3:3, males in group B mated more than those in similar cage ratios in group A. As the male to female ratio decreased, the copulation frequency per male increased in both groups, thus following a regular pattern in relation to the increased presence of females. This increase in mating was perhaps due to reduced competition among the males and to the increased availability of females, which afforded greater opportunity for mating. Groups A and B both averaged the highest number of matings per female, 8.5 and 15.5, respectively, at the 4:2 ratio. The copulation frequency of the

Table 1.—Average copulation frequencies for both sexes of *A. elliotti*, and average egg production per female, in groups maintained at selected sex ratios both in a greenhouse (group A) and adjacent outdoors (group B).

Ratio ♂ : ♀	Avg copulation frequency ♂	Avg copulation frequency ♀	Avg no. eggs/♀
	Group A		
5:1	1.3	6.5	8.5
4:2	4.3	8.5	1.2
3:3	6.8	6.8	4.1
2:4	10.0	5.0	14.2
1:5	18.0	3.6	1.9
0:6	—	0	4.3
	Group B		
5:1	1.1	5.5	23.5
4:2	7.7	15.5	12.7
3:3	6.7	6.7	39.7
2:4	11.5	5.7	57.4
1:5	29.0	5.8	39.6
0:6	—	0	2.5

females in group A increased along with an increase in the number of males, except at the 5:1 ratio, where the number of copulations per female decreased (Table 1). In group B the copulation frequency of the females followed a similar pattern, except for the 1:5 ratio, which was slightly higher than the 2:4 ratio. It was interesting to note that the average copulation frequency per female at the 5:1 ratio in both groups was lower than expected when comparing it with the other ratios. Perhaps at this sex ratio, competition between males was more intense and/or perhaps the female's receptivity or behavior was affected by the increased presence of the more active males. Renner (1952) stated that the receptivity of *Euthystira brachyptera* Osten Sacken, a species of grasshopper, varied according to the reproductive condition of the females. He noted that females became unreceptive 2 days prior to egg laying and that after egg laying they became receptive until ready to oviposit again. In this study, females which had mated were frequently observed to avoid further copulation by vibration of their hind femora and/or elevating their abdomen.

The Influence of Copulation on Egg Production.—The average copulation frequency and average number of eggs produced per female in both groups A and B is presented in Table 1. In group A, egg production was lowest at the 4:2 ratio with an average of 1.2 eggs/female, while the average number of matings was the highest, or 8.5 matings/female. The greatest number of eggs were produced at the 2:4 ratio, 14.2 eggs/female, where the average copulation frequency per female was the second lowest of any ratio, 5.0. Unmated females at the 0:6 ratio produced an average of 4.3 eggs/female, which was higher than the number produced at the 4:2, 3:3, and 1:5 ratios.

In group B, the highest average number of eggs per female, 57.4, was produced at the 2:4 ratio where the frequency of mating was second lowest, 5.7 matings/female. Females at the 4:2 ratio averaged the highest number of matings, 15.5, and laid the fewest average number of eggs per mated female, 12.7. Egg production per female at the 0:6 ratio was 2.5 eggs, the lowest of all ratios.

In both groups A and B, the copulation frequency was highest for females held at the 4:2 ratios and egg production lowest, considering only those ratios with males (Table 1). Conversely, the greatest average number of eggs per female was produced at the 2:4 ratios where the frequency of mating was second lowest in both groups. The constant disturbance by the males probably caused physical stress in the females, which may have interfered with egg production and oviposition at the 4:2 ratios, while the amount of mating activity at the 2:4 ratio apparently provided suitable conditions for maximum egg production in this study. At all sex ratios, except 0:6, the females in group B, which were exposed to more natural environmental conditions than those in group A, produced more eggs per female. The size difference of the cages may have contributed to the variations in copulation frequency and egg production. Norris (1959) reported females of the red locust, *Nomadacris septemfasciata* Serville, maintained under crowded conditions laid fewer eggs than females of isolated pairs. Likewise, Barnes (1965) stated that females of the migratory grasshopper, *Melanoplus sanguinipes* (F.), produced increasingly fewer eggs as the density of adults increased. Cages used in this study in group A theoretically contained 54 grasshoppers/1-yd^2 surface area compared with 6/1 yd^2 for those in group B. Possibly the heavier density of grasshoppers and the more artificial conditions in the cages in group A caused a reduction in egg production through some physiological influence. Also, females in groups A often deposited frothy egg masses on the wooden bases of cages, while those outdoors did not. Anderson and Hastings (1966) reported that females of the big-headed grasshopper preferred undisturbed rather than sifted soil from their natural habitat for oviposition, apparently because the females were unable to grip the loose surface with their hind tarsi. Females of the big-headed grasshopper in this study oviposited freely in the firm, natural clay-loam soil in the cages in group B situated outdoors, even though it was in an environmental area different from that of their natural rangeland environment, while those in group A in the greenhouse cages appeared to have difficulty ovipositing in the loose, sifted clay-loam soil provided them.

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